# Growth models for small-scale forest utilization in Papua New Guinea

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#### Abstract

Utilization of tropical forests is increasingly occurring in small-scale community-based operations. This is the case in Papua New Guinea (PNG) where community-based operations are seeking Forest Stewardship Council (FSC) certification. To examine whether these operations are sustainable, for evaluating scenarios, and for quantifying impacts on carbon stocks and other forest values, growth models are required for predicting tree growth and carbon sequestration at the scale of the individual tree. Based on a large Permanent Sample Plot (PSP) database growth models are being developed that characterize the growth and competitive dynamics of individual trees. In this paper we quantify competition indices and test their applicability in mixed tropical forests. Aside from growth prediction, competition indices may also provide a basis for grouping tropical tree species into guilds with similar attributes. This can simplify growth model between fast growing shade-intolerant pioneer species such as *Macaranga* and slower growing shade-tolerant climax species such as *Pometia Pinnata* (Taun). These important insights can guide further growth model development.

# Key words

Growth model, Species classification, Forest dynamics, Tropical rain forest, Shade tolerance

# Introduction

The degradation of tropical forests is often associated with poor knowledge of the goods that may be available, and ignorance to the benefits of sustainable management. This is the case in Papua New Guinea (PNG) where assessment of goods such as timber and carbon, and the benefits of sustainable management and certification need to be communicated to land-owning communities. They can then make informed decisions and derive sustainable benefit from their resource. A large project funded by the Australian Centre for International Agricultural Research (ACIAR) is underway developing forest assessment tools for tropical forests in PNG integrating remote sensing, geographic information systems and forest growth modeling. These tools can assist with forest certification efforts in community forestry. In this paper we focus on the development of individual-tree growth models for PNG based on an extensive database of Permanent Sample Plots (PSPs).

Forest utilization in PNG is increasingly occurring at the community level using smallscale sawmills to extract individual trees. This small-scale utilization is the basis of Forest Stewardship Council (FSC; an international body that outlines the social, environmental and economic requirements for certification) certification efforts that aim to empower landowners, improve livelihoods, preserve the natural environment, whilst facilitating sustainable development (Bun & Scheyvens 2007). To examine whether these operations are sustainable growth models are required for predicting tree growth at the scale of the individual tree. Many alternative growth and yield modeling methodologies exist (e.g. Vanclay 1994). The individual-tree approach has been selected here as it matches the scale of utilization and is sufficiently flexible to accommodate mixed-age and mixed-species tropical forest. Most importantly individual-tree models inform; smallscale (individual-tree) scenario analysis; growth and yield estimates which are fundamental to sustainable forest management; species-specific carbon sequestration; impact of small-scale utilization on carbon stocks.

The United Nations Framework Convention on Climate Change (UNFCCC) has endorsed an initiative to Reduce Emissions from Deforestation and Degradation of forests (REDD) in developing countries. There has been much interest in applying the REDD initiative in PNG. However, much technical work on quantifying carbon stocks, and carbon sequestration is required before the REDD initiative can become operational. This study hopes to contribute to this, with the development of species-specific growth and carbon sequestration models. Species specific models are important because tropical forest trees vary greatly in wood density and growth rates; two important determinants of carbon stock and sequestration rates. The consequences of small-scale community utilization on carbon stocks can then be explicitly quantified, forest management scenarios can be evaluated in terms of their impact on carbon stocks, and scenarios for alternative revenue from carbon under the REDD initiative can be explicitly quantified.

Individual-tree growth models characterize the growth and competition dynamics of individual trees; this is challenging in the complex and diverse tropical forests of PNG. This paper will outline preliminary work quantifying the competitive influences affecting individual trees, and how this relates to tree growth. Competition indices have been the subject of much attention in the forestry literature. Distance-dependent indices use the spatial positions of individual trees in their formulations whereas distance-independent indices do not. Because distance-dependent indices incorporate the spatial pattern of competitors, it should follow that they provide an improved quantitative expression of competition. The various competition indices can be organized into several groups. Distance-dependent indices consist of distance weighted size ratio indices (e.g. Hegyi 1974), area overlap indices (e.g. Bella 1971), and area potentially available indices (e.g. Nance et al. 1987). Distance-independent indices consist of functions of subject tree attributes compared to the attributes of other trees on the plot (e.g. Stage 1973), and stand-level indices such as basal area per hectare and stems per hectare. The various competition indices described above have been quantified for 85,000 trees from a large PSP database in PNG, and will be compared in terms of their ability to predict tree growth.

Tropical forests are characterized by a high diversity of woody species, and no universally applicable species groupings exist that capture the continuum of growth dynamics (Clark and Clark 1999). However, there is a need to group species for the development of forest growth models as grouping similar species increases the sample size, reducing parameter variance, and resulting in fewer and more parsimonious models. Grouping similar species is also important in the ecological insights they can offer on species growth habits. Ever since Whitmore (1975) first described tropical tree functional groups (fast growing shade-intolerant pioneers, and slower growing shade-tolerant climax species) researchers have been attempting to group species using a variety of strategies (reviewed by Gourlet-Fleury et al. 2005). Data driven methods for grouping species have used tree attributes such as wood density, growth rate, life-span, and potential size (Gourlet-Fleury et al. 2005). Alder (1997) used adult diameter (90<sup>th</sup> quantile of diameter distribution) and mean diameter increment as the basis of a 2-dimensional ordination for species in Papua New Guinea. This resulted in 21 species groups; the faster growing groups included pioneer and ephemeral species, whilst slower growing groups consisted of some larger shade-tolerant species with dense heavy timber (Alder 1997). Preliminary work on an alternative basis for grouping PNGs tree species will be presented here.

It would be expected that species-specific response to competition would be highly diverse in the tropical forests of PNG and should correlate with species growth habits such as those described by Whitmore (1975). Based on the analysis of species specific competition response there is an opportunity to group species into 'competitive guilds'. If species can be successfully grouped, fewer and more parsimonious models can be estimated that are more easily applied in forest management contexts. Possibilities for this will be explored in this paper.

The disentanglement of growth and competition dynamics in the forests of PNG is an important first step toward the development of individual-tree models of growth and carbon sequestration that can inform small-scale community forest utilization.

# Materials and Methods

#### PSP database

Over the last 20 years Papua New Guinea Forest Research Institute has established and remeasured over 125 permanent sample plots (PSP) across PNG covering all major forest types. Each plot is one hectare in size and is divided into 25 sub-plots of 20 m x 20 m. The spatial location, diameter, height, and crown characteristics are recorded for all trees over 10cm. The PSP database represents a strong basis for the development of individual-tree growth models. Because individual trees in PSPs are spatially mapped, we can extricate the spatial competitive processes governing tree growth.

# Distance weighted size ratio competition indices

The distance weighted size ratio (DWSR) competition indices include those that use the distance between trees weighted by their respective sizes in their formulations. Two for the most successful DWSR variants were quantified in this study and include that of

Hegyi (1974) and Newnham (1966). The index of Newnham quantifies local density as the sum of angles subtended from the subject to either side of the stems of competitors. The two DWSR indices are described in Table 1.

| Index | Formulation   | Author         |
|-------|---|----------------|
| HEG   | $HEG_i = \sum_{j=1}^{n_i} \left[ \frac{D_j}{D_i} \times \frac{1}{Dis_{ij}} \right]$ | Hegyi (1974)   |
| NEW   | $NEW_i = \sum_{j=1}^{n_i} 2 \left[ a \tan \frac{0.5D_j}{Dis_{ij}} \right]$          | Newnham (1966) |

Table 1. Distance Weighted Size Ratio competition indices.

Where;  $n_i$  = total number of competitors for the subject i,  $D_i$  = diameter at breast height for the subject tree i, Dj = diameter at breast height of the  $j^{th}$  competitor,  $Dis_{ij}$  = the distance in meters between the subject i and competitor j,

The choice of which competitors to include when calculating DWSR indices is an unresolved problem (Burton 1993). To reduce subjectivity in estimates of competitor search radius, a methodology was used whereby an optimal search radius (OSR) was identified mathematically for each species. This could also provide insight into the range of the competitive dynamic affecting particular rainforest species. By examining the relationship between index performance and competitor search radius, it was confirmed that generally index performance approached a maximum value asymptotically. The point at which performance first began to level off was then estimated mathematically using a segmented, non-linear equation similar to the spherical semivariogram employed in geostatistics (e.g. Journel and Huijbregts 1978). This segmented, non-linear model was fitted to characterize the relationship between correlation of the index with growth and competitor search radius and can be described as:

$$Corr_{i} = \alpha \left[ 1.5(sr_{i} / \beta) - 0.5(sr_{i}^{3} / \beta^{3}) \right], \qquad sr_{i} \leq \beta$$
$$Corr_{i} = \alpha, \qquad \qquad sr_{i} > \beta \qquad (1)$$

Where;  $sr_i$  is the search radius (i = 2 to 20 meters at 2 meter increments),  $Corr_i$  is the correlation between the competition index and annual diameter increment for search radius i, and  $\alpha$  and  $\beta$  are parameters estimated using the NLIN procedure in SAS (SAS Institute Inc. 1996).  $\alpha$  can be interpreted as an estimate of the maximum correlation and  $\beta$  interpreted as an estimate of the OSR.

#### Area overlap competition indices

The area overlap (AO) indices were formally introduced by Opie (1968), but the most successful formulation was presented by Bella (1971) as:

$$AO_{i} = \sum_{j=1}^{n_{i}} \left[ \left( \frac{ZO_{ij}}{Z_{i}} \right) \left( \frac{D_{j}}{D_{i}} \right)^{EX} \right]$$
(2)

Where;  $AO_i$  is the AO index of Bella (1971) for tree *i*,  $Z_i$  is the area of the 'zone of influence' of the subject tree *i*,  $ZO_{ij}$  is the area of 'zone of influence' overlap between the subject *i* and competitor *j*. *EX* is the exponent applied to ratios, and previous studies have identified the optimal exponent as being between 1 and 3 (e.g. Bella 1971).

The AO indices use a function of the area of overlap between a subject's and a competitor's 'zone of influence' to quantify competition. Their success depends on a suitable estimate of 'zone of influence' which is defined as the total area over which a tree obtains or competes for resources (Opie 1968). We use a prediction of crown area to quantify the zone of influence of each tree. Studies on the zone of influence have found that the area over which a tree obtains or competes for resources for resources is approximately equivalent to the area enclosed by 2 crown radii (e.g. Bi and Jurskis 1996). This approximation was used to estimate the 'zone of influence' as:

$$RZ_{i} = 2 \times \sqrt{\frac{\left(PA \times (D_{i} / \sum_{j=1}^{t} D_{j})\right)}{\pi}}$$
(3)

Where; RZi is the radius of the 'zone of influence' for tree *i*, *PA* is the plot area, and *t* is the total number of trees on the plot. The relationship of (3) partitions total plot area into individual tree crown areas dependent on the size of each tree.

#### Area potentially available competition indices

The area potentially available (APA) indices, first introduced in the forestry literature by Brown (1965), are derived from the classical Voronoi diagram. The Voronoi diagram is a continuous tessellation of an area into non-overlapping polygons. Brown (1965) introduced APA indices to forestry as a means of quantifying the area potentially available for growth, and they have since been widely adopted as competition indices. Several variants exist, including the weighted APA (Moore et al. 1973) and the weighted and constrained APA (Nance et al. 1987). The weighted APA (Moore et al. 1973) weights the position of the perpendicular bisector on the line joining a tree to its competitor by a ratio of tree sizes. Nance et al. (1987) proposed a weighted and constrained APA to curtail the development of large irregular polygons when spatial arrangements become irregular. When constructing the tessellation they selected the smaller of the distance to the polygon boundary or the output of a constraining function. Nance et al. (1987) proposed a function of crown radius as a constraining function, and this was realized using a constraining function based on the predicted crown radius for the subject tree as described in (3). Three variants of the APA index are described in Table 2.

Table 2. Area potentially available competition indices.

| Index | Weighting function  | Constraining function  | Author                     |  |
|-------|---|--|----------------------------|--|
| APA   | -   | -  | Brown (1965)               |  |
| APAW  | $DB_{ij} = \left[\frac{D_i^2}{(D_i^2 + D_j^2)}\right] Dis_{ij}$ | -  | Moore <i>et al.</i> (1973) |  |
| APAWC | $DB_{ij} = \left[\frac{D_i^2}{(D_i^2 + D_j^2)}\right] Dis_{ij}$ | $CF_{i} = \sqrt{\frac{(PA \times (D_{i} / \sum_{j=1}^{t} D_{j}))}{\pi}}$ | Nance <i>et al.</i> (1987) |  |

Where;  $DB_{ij}$  = the distance to the perpendicular bisector located on the straight line between the subject *i* and competitor *j* 

The APA class of competition indices is the most complex to compute. A SAS Macro (SAS Institute Inc. 1990) was written for efficient computation of all APA variants along with DWSR, AO, and distance-independent. SAS Macros for quantifying the various competition indices detailed in this study are available upon request from the primary author. An example of the weighted and constrained APA (APAWC) for the Krisa PSP plot is shown in Figure 1. The spatial irregularity of the PSP plot can be observed.

Figure 1. Graphic of the weighted and constrained APA for the Krisa PSP plot



# Alleviating boundary effects

A boundary effect is generated when boundary trees are subject to competition from outside the plot that is not incorporated in competition indices. To minimize information loss from exclusion of trees subject to edge effects, we used a toroidal edge correction scheme commonly used in spatial statistical applications (Ripley 1981). Toroidal edge correction is implemented by considering a rectangular spatial array as a torus. This can be realized simply by translating the spatial arrangement to create eight new adjoining arrays. The validity of toroidal edge correction depends upon the assumption that boundary trees are subject to equivalent competition from both outside and inside the plot which is tenuous for trees close to the boundary in an irregularly structured tropical forest, i.e., less than 5 meters. But it should be permissible for trees more than 5 meters from the boundary. Following this trees within 5 meters of the boundary were excluded from analysis and toroidal edge correction was applied to all other trees.

#### Distance-independent Competition indices

Distance-independent indices consist of functions of subject tree attributes compared to the attributes of other trees on the plot (Stage 1973). They do not use spatial information. The index developed by Stage (1973) was quantified;

$$DAL_i = \sum_{i=1}^{n_i} D_i \tag{4}$$

#### Evaluating competition indices

Competition indices were evaluated for their ability to predict annual diameter increment in the next growing period using two criteria. The first criterion was the correlation between the index and annual diameter increment in the next growing period. If the relationship between each variable and annual diameter increment was found to be nonlinear, a transformation was sought which rendered the relationship linear. In these instances the fit of the transformed variable was evaluated.

The second criterion was the significance of the competition index as fixed effect in a mixed model with basal area against annual diameter increment. Basal area was included as a fixed effect to extricate the influence of differing stand density on tree growth. A mixed model was used to account for the nested dependence (Fox et al. 2001) affecting PSPs; the growth of trees within each PSP will be more similar than that between each PSP, as trees on the same plot will be subject to the same local environmental conditions, and will be of a similar forest type. To account for this a random effect was used for each PSP measurement. This will ensure correct statistical inference on the growth and competition dynamics within and between PSP plots (Fox et al. 2001).

#### **Results and Discussion**

#### Optimal competitor search radii

Different trends in correlation across different search radii emerged for different species. An example of the fitted non-linear model for Hegyi's (1974) index is shown in Figure 2. For *Pometia Pinnata*  $\alpha$  was estimated as 0.12, and  $\beta$  was estimated as 13.7. These can be interpreted as an asymptotic correlation of 0.12, and an optimal search radius of 13.7 meters.



Figure 2. Fitted non-linear model for estimating optimal competitor search radius for *Pometia pinnata*.

Estimated optimal search radii (OSR) for different species are detailed in Table 4. It can be observed that some species such as *Calophyllum* have small OSR values (3 m), while other species such as *Horsfieldia* have large OSR values (20m). These results suggest that the range of the competitive effect is different among tropical species. For example, it could be hypothesized that *Calophyllum* is most affected by competition for light among immediate neighbors (competitors within 3 meters) whilst for *Horsfieldia* competition for light and nutrients is more diffuse and occurring over a larger area (up to 20 meters). Future work will attempt to relate OSR values to the shade-tolerance of different species. We would expect that species with small OSR values that are most effected by competition for light are shade-intolerant, while species with large OSR with a more diffuse competitive affect are shade-tolerant.

# Evaluating competition indices

10 competition indices were quantified for approximately 85,000 individual tree measurements across the 125 permanent sample plots. The 300 most numerous species on PSPs were selected for specific study of competition indices. Preliminary analysis was used to identify a subset of competition indices for further study. The best performing indices were selected on the basis of strength of correlation with tree growth across the 300 species. The following subset was identified for further study;

- DBHOB (Diameter at Breast Height Over Bark)
- DAL (Sum of Diameter in trees of larger diameter than the subject)
- SQAPAWC (Square Root of APASWC)
- LNNEW (Natural Logarithm of NEW)
- LNAO1 (Natural Logarithm of AO with exponent 1)

The best performing competition index was then identified for each of the 300 species. Table 3 shows the competition indices ranked for the percentage of the 300 species for which they were optimal (in terms of correlation with annual diameter increment). Table 3 also shows the competition indices ranked for the number of times they were optimal in terms of fixed effect significance in a mixed model with basal area across the 300 species

|                   | Correlation - Percentage of species | Mixed model - Percentage of |  |  |  |  |
|-------------------|-------------------------------------|-----------------------------|--|--|--|--|
| Competition Index | optimal                             | species optimal             |  |  |  |  |
| DBHOB             | 14                                  | 18                          |  |  |  |  |
| DAL               | 28                                  | 21                          |  |  |  |  |
| SQAPAWC           | 15                                  | 13                          |  |  |  |  |
| LNNEW             | 29                                  | 29                          |  |  |  |  |
| LNAO1             | 14                                  | 19                          |  |  |  |  |

Table 3. Percentage of species for which each competition index was optimal

Table 3 demonstrates that no single competition index is optimal across the 300 species. It also demonstrates that distance-independent indices such as DBHOB and DAL are equally as effective as distance-dependent indices. DAL (28%, 21%) and LNNEW (29%, 29%) appear to be optimal most often across the 300 species. when basal area was included as a fixed effect in a mixed model, distance-dependent indices performed better (optimal for 61% of indices). This may be due to basal area characterizing stocking differences across PSPs, and negating the influence of the distance-independent index DAL (28% down to 21%).

Diameter performed well as a predictor of growth performing better than competition indices for 14% & 18% of species. This is in agreement with previous studies that have found that diameter is an excellent predictor of growth (Lorimer 1983). Diameter can be considered a historical log of past competitive interactions, genotypic differences, and localized environmental heterogeneity, and therefore tends to be strongly correlated with future growth.

Failure to identify a single index as optimal in the mixed tropical forests of PNG could be associated with variability in competition response across the 300 species. Shade-intolerant species will compete strongly with first order neighbors for light and nutrients. The SQAPAWC most accurately characterizes these first order interactions. The LNAO1, and LNNEW competition indices may perform better for more shade-tolerant species as competition for light and nutrients would be more diffuse, less intense, and be occurring over a larger area. Following this hypothesis, distance-independent indices such as DAL and DBHOB would perform well for very shade-tolerant species for which the location and size of nearby competitors is relatively unimportant. Future work will attempt to align the shade tolerance of different species with the performance of different competition indices.

To provide more detail of competition index performance, Table 4 provides further statistics for a subset of the 16 most observed species.

| Species                       | Obs  | Optimal<br>Search<br>Radius | Optimal<br>Corr | Corr  | Optimal<br>Mixed | Effect<br>Sig | Wood<br>Density | Diameter<br>90 <sup>th</sup> Quan | Mean<br>Incr |
|-------------------------------|------|-----------------------------|-----------------|-------|------------------|---------------|-----------------|-----------------------------------|--------------|
| Calophyllum sp.               | 1072 | 3.0                         | DAL             | -0.16 | DAL              | 4.0E-03       | 0.50            | 47.0                              | 0.53         |
| Canarium sp.                  | 2323 | 6.9                         | DAL             | -0.20 | DAL              | 6.3E-08       | 0.48            | 36.5                              | 0.42         |
| Celtis sp.                    | 990  | 5.5                         | LNNEW           | -0.21 | DAL              | 2.0E-04       | 0.55            | 50.0                              | 0.52         |
| Cryptocarya sp.               | 1993 | 7.4                         | DAL             | -0.09 | LNAO1            | 6.0E-02       | 0.46            | 34.7                              | 0.44         |
| Dysoxylum sp.                 | 1846 | 14.2                        | DAL             | -0.20 | DAL              | 3.0E-17       | 0.62            | 39.9                              | 0.38         |
| Ficus sp. (Fig)               | 1536 | 5.9                         | DAL             | -0.20 | DBHOB            | 2.9E-10       | 0.34            | 45.5                              | 0.51         |
| Garcinia sp.                  | 1018 | 11.8                        | LNNEW           | -0.16 | LNNEW            | 1.1E-04       | 0.64            | 31.5                              | 0.37         |
| Horsfieldia sp.               | 1682 | 20.0                        | LNNEW           | -0.14 | LNNEW            | 1.3E-04       | 0.36            | 31.2                              | 0.35         |
| <i>Litsea</i> sp.             | 1022 | 5.7                         | DAL             | -0.25 | LNAO1            | 7.3E-11       | 0.40            | 38.4                              | 0.51         |
| Macaranga sp.                 | 1426 | 14.3                        | DAL             | -0.27 | LNNEW            | 9.5E-12       | 0.30            | 22.8                              | 0.96         |
| <i>Myristica</i> sp. (Nutmeg) | 3113 | 9.6                         | DAL             | -0.16 | LNNEW            | 1.4E-03       | 0.38            | 25.7                              | 0.31         |
| Pimeleodendron<br>amboinicum  | 1745 | 15.7                        | LNNEW           | -0.17 | DBHOB            | 3.2E-07       | 0.48            | 39.8                              | 0.42         |
| Planchonella sp.              | 1683 | 9.0                         | LNNEW           | -0.21 | LNAO1            | 4.9E-09       | 0.45            | 37.6                              | 0.44         |
| Pometia pinnata<br>(Taun)     | 2777 | 13.7                        | LNAO1           | -0.16 | LNAO2            | 2.6E-10       | 0.58            | 54.4                              | 0.67         |
| Syzygium sp.                  | 2854 | 10.8                        | DAL             | -0.17 | DAL              | 4.1E-12       | 0.61            | 41.1                              | 0.37         |
| Terminalia sp.                | 638  | 8.3                         | DAL             | -0.21 | LNAO1            | 3.4E-07       | 0.45            | 46.3                              | 0.67         |

Table 4. Competition index performance and other statistics for the 16 most observed species on PSP plots

Where; Obs is the number of observations, Optimal Corr is the competition index with optimal correlation against annual diameter increment whilst Corr is the Spearman's correlation coefficient, Optimal Mixed is the competition index with optimal effect significance in a mixed model and Effect Sig is the t test that the parameter is significantly different to zero, Wood Density is Basic Density; the weight of wood at 0% moisture content occupying one cubic meter (units:  $10^3 \text{ kg/m}^3$ ) from Eddowes (1977), Diameter 90<sup>th</sup> Quan is the 90<sup>th</sup> quantile of the diameter distribution, and Mean Incr is the average annual diameter increment in the next growing period.

Analysis for the 16 most observed species again indicated that no single competition index is dominant, with indices DAL and LNNEW performing well. The optimal index for each species explained only a modest amount (14-27%) of the variability in diameter increment. However, indices were highly significant when evaluated in a mixed model with basal area per hectare.

Table 4 also provides insights into tree attributes that could be used as a basis for species grouping. Wood density, growth rate, and potential size have been used in other studies to group species. *Macaranga* is a pioneer species with the largest growth rate (0.96 cm/yr), smallest potential size (22.8 cm), lowest wood density (300 kg/m<sup>3</sup>), and the strongest correlation for competition indices (0.27). This is congruent with previous findings that pioneer species tend to be fast growing, tend have small potential size, low wood density, and tend to be shade-intolerant with a life cycle characterized by rapid growth to capitalize on canopy gaps. Intolerance to shade from nearby trees explains the importance of competition indices in explaining future growth. In contrast to this *Pometia Pinnata* (Taun) is a climax species with a slower growth rate (0.67 cm/yr), large potential size (54.5 cm), denser wood (580 kg/m<sup>3</sup>), and weaker correlation for competition indices

(0.16). Again, this is congruent with climax species being slower growing, having larger potential size, denser wood, and being more tolerant of shade from nearby trees. More tolerance to competition explains the weaker correlation of competition indices with future growth. The local spatial arrangement of soil fertility, topographic, geologic and climatic factors will be more important in explaining growth for shade-tolerant species. Other species in Table 4 fall on the continuum between pioneers such as *Macaranga* and climax species such as *Pometia Pinnata*. This brief analysis suggests that competition response as characterized by competition indices could be used as an additional attribute for species groupings in tropical forests.

Tree growth is a complex process. It is influenced by an intricate network of above- and below-ground competitive interactions as well as the local spatial arrangement of soil fertility, topographic, geologic and climatic factors. The vast majority of current competition indices and growth models remain overly simplified (Fox et al. 2001). This over-simplification results in large amounts of unexplained variability, and growth modelers have come to accept this as an 'occupational hazard' (Burkhart and Gregoire 1994). Competition indices explained at best 25% of the variability in individual tree growth in mixed tropical forest in PNG. Future work requires insights into this unexplained variability that can improve growth model performance. Despite these shortcomings, the competition indices examined here, and the insights into competitive dynamics they provided, can guide further growth model development for mixed tropical forest in PNG.

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